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Short-term responses of soil and litter invertebrates to a cool autumn burn in Jarrah *(Eucalyptus marginata)* forest in Western Australia

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With 14 figures

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1. Introduction

Throughout many parts of Australia forests and woodlands are subjected to low intensity prescription burns or to wildfires whose intensities are respectively less than 300 kW m^{-1} and often in excess of 50,000 kW m^{-1} (Vines 1981). It is important to understand the effect these fires have on the soil and litter invertebrates since these animals have a direct, or regulatory, role in litter decomposition and therefore in nutrient cycling (Reichle 1977, Kitchell *et al.* 1979) and they also play an important part in maintaining soil structure (Abbott *et al.* 1979). A few attempts to quantify the influence of fire in Australia on soil and/or litter invertebrates have been made (reviewed in Campbell & Tanton 1981) and most have adopted widely differing approaches. McNamara (1955) drew inferences on the effects of fire by comparing soil and litter invertebrates in a protected compartment and annually burnt fire breaks within the Western Australian Jarrah (*Eucalyptus marginata* Donn *ex.* Sm.) forest. Springett (1976) adopted a similar approach when she compared soil mesofauna in Jarrah and Karri (*Eucalyptus diversicolor* F. Muell.) forest blocks which had been subjected to prescription burning or had been protected from fire for considerable periods. In a study of Karri forest litter fauna Hindmarsh & Majer (1977) introduced a time component by selecting forest compartments which had been burnt 0.5, 5, > 20 and > 40 years previously. Springett's (1979) study of the effects of a hot summer fire in Jarrah introduced a further approach when she sequentially resampled the same site 14, 15 and 16 months after the burn. Pre-fire invertebrate populations were not assessed in any of the above montioned Western Australian studies.

Campbell & Tanton (1981) recently reported a detailed investigation of soil and litter invertebrate responses to burning in *Pinus radiata* D. Don and *Eucalyptus* spp. forests close to Canberra in the Australian Capital Territory. They selected five plots in each of the two vegetation types and, after at least two samplings had been completed, burnt three pine and three eucalypt plots. The invertebrates were then sampled several times after the fire, sorted into broad taxonomic units, and the data analysed by various multivariate techniques. They concluded that the inter-site and seasonal variability of the data were as great as that associated with the burn treatments. Also, invertebrate recovery to levels within the range of variation of unburnt sites was quite rapid following the fire they investigated.

The following study offers an additional approach to understanding the influence of fire on soil and litter invertebrates. Here the soil and litter fauna was sampled in one plot for 1 month prior and 13 months after a cool autumn prescription burn. Samples were taken simultaneously from a similar, but unburnt, plot. An almost identical experimental approach has been adopted by Athias (1976) during a study of soil microarthropods in burnt and unburnt plots in the Ivory Coast. The present study involved separate sampling of the soil and litter mesofauna.

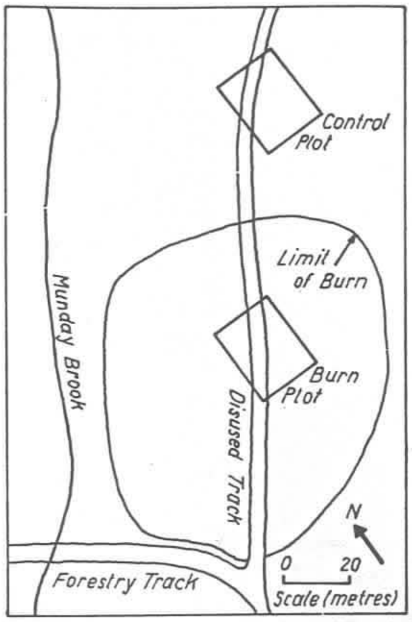

Fig. 1. Map of the Karragullen study area showing the insect study plots and limit of the March 1978 prescription burn.

2. Materials and methods

2.1. Experimental study area

The study area was situated near Karragullen in the Forests Department Victoria Block (32° 04′ S, 116° 07′ E, Grid AZ 65 on Forests Department Mundaring 80 map). The vegetation consisted of open sclerophyllous forest dominated by Jarrah and an admixture of Marri (*Eucalyptus calophylla* R. Br. *ex.* Lindl.). There was a dense shrub understorey with a scattered lower tree storey (*Banksia* spp. and *Persoonia longifolia* R. Br.). The soil was a lateritic, well drained gravel and the climate was typically Mediterranean with cool, wet winters and hot, dry summers. The site was previously prescription burnt in the spring of 1975 and the forest was generally healthy although Jarrah dieback, caused by *Phytophthora cinnamomi* Rands, had affected vegetation in nearby low-lying areas. The study area occupied gently sloping ground adjacent to Munday Brook (Fig. 1).

During January, 1978, two 20 × 25 m plots were marked out within the study area (Fig. 1). The plots were situated at the eastern and western ends of the study area and were selected for their similarity of vegetation, soil and litter composition. Each plot was gridded at 5 m intervals in order to form the basis of subsequent stratified-random sampling procedures. The plots were designated "burnt" and "unburnt" plot.

The burnt plot and a surrounding buffer zone were burnt by the Western Australian Forests Department on 29 March, 1978. The fire varied in intensity throughout the plot although the most common intensity range was calculated by the Byram (1959) formula to be between 150—200 kW m^{-1}. Vertically buried slates supporting lines drawn with chalks of varying melting points indicated that soil temperatures reached 38 °C down to 22—75 mm, 45 °C down to 10—57 mm and 66 °C down to 5—12 mm. One slate showed penetration at 66 °C down to 35 mm.

The burn resulted in partial ashing of the litter layer and localised scorching of the mineral soil. All leaves of the ground cover species were burnt, the understorey defoliated, and the tree stems and overstorey crowns were scorched throughout the area. Leaves from the scorched crown fell soon after the fire.

2.2. Physical and botanical measurements

Most recordings were taken from early March, 1978, prior to the experimental burn, until April, 1979.

Mean monthly rainfall, maximum and minimum temperatures were obtained from the Forests Department Mundaring Weir station which is situated 14 km north of study area. Rainfall data have since been obtained from the Bureau of Meteorology rainfall station at Karragullen and both the magnitude and distribution of rain have been found to be similar at the two stations. The monthly meteorological data values are shov

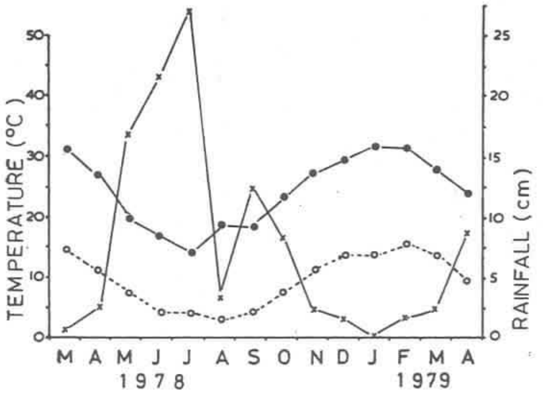

Fig. 2. Monthly rainfall (×———×), mean monthly maximum temperature (●———●), and minimum temperature (○---------○) for the Forests Department Mundaring Weir recording station.

Ten points were selected per month in each plot by a stratified random method. These were used for the measurements of soil temperature, air temperature, relative humidity and litter mass. Soil temperature was measured 5 cm beneath the mineral soil surface and air temperature 5 cm above ground level. Relative humidity was obtained using a wet and dry bulb thermometer placed 5 cm above ground level. All meteorological recordings were taken during mid-morning and the recording apparatus were always shaded from the direct effects of sunlight.

Litter mass was recorded in the burnt and unburnt plots prior to the burn in March, 1978, and then from July, 1978 onwards. All litter was collected from ten 19×19 cm quadrats situated at the spots where meteorological data had been recorded. Samples were then dried to constant mass in ovens set at 50 °C and the results were expressed as kg dry mass of litter m^{-2}.

Soil and litter samples were taken during early morning from the unburnt plot at monthly intervals for moisture determination. Five points were selected per month on a stratified-random basis and the litter first removed from 19×19 cm quadrats. The litter was sealed in plastic bags and then 54 mm diameter, 97 mm deep soil cores were taken from the same spot. These were sealed in tins. Following weighing the litter was dried at 50 °C and the soil at 120 °C. After constant mass was achieved the percentage moisture content of the litter and soil was calculated.

2.3. Invertebrate samples

In both plots, the soil and litter mesofauna were sampled from ten stratified randomly selected points per month between March, 1978, prior to the burn, until April, 1979. At each of the ten points in each plot the litter was removed from a 19×19 cm quadrat and sealed in polyethylene bags. Soil cores (54 mm diameter, 97 mm deep) were then taken from beneath the litter and the soil extruded into 54 mm internal diameter plastic sleeves which had a 3 mm mesh base. Both sets of samples were immediately returned to the laboratory and the soil fauna extracted using a multiple canister heat extractor (Southwood 1966) in which the temperature was raised from ambient to 40 °C over a 1 week period.

Why? No damage to soil animals?

Only two Berlese funnels were available so the ten litter samples from respective plots were bulked, mixed and placed in the two funnels. The 19×19 cm litter quadrats were one tenth of the area of the Berlese funnel mesh which meant that litter in the funnel was the same thickness as on the forest floor. Each funnel supported a 43×43 cm mesh which had a 1.2×1.6 mm hole size. This prevented small litter fragments falling into the alcohol preservative but prevented the passage of large litter animals. Consequently the central small mesh was surrounded by a 8.5 cm boundary of 6×6 mm mesh hole size to allow the passage of larger animals. The temperature above the litter was raised from ambient to 40 °C over a 1-week period.

The invertebrates from the soil and litter samples were sorted and counted to the class and/or order level. The semi-sorted monthly samples are currently stored in 70% ethanol (alcohol) and are housed at the School of Biology, Western Australian Institute of Technology.

3. Results

3.1. Physical changes in the soil and litter

The pre-burn soil temperature was lower in the burnt than in the unburnt plot although this difference was immediately reversed following the fire (Fig. 3a). Burnt plot soil remained the warmest for the duration of the observations and differences were significant

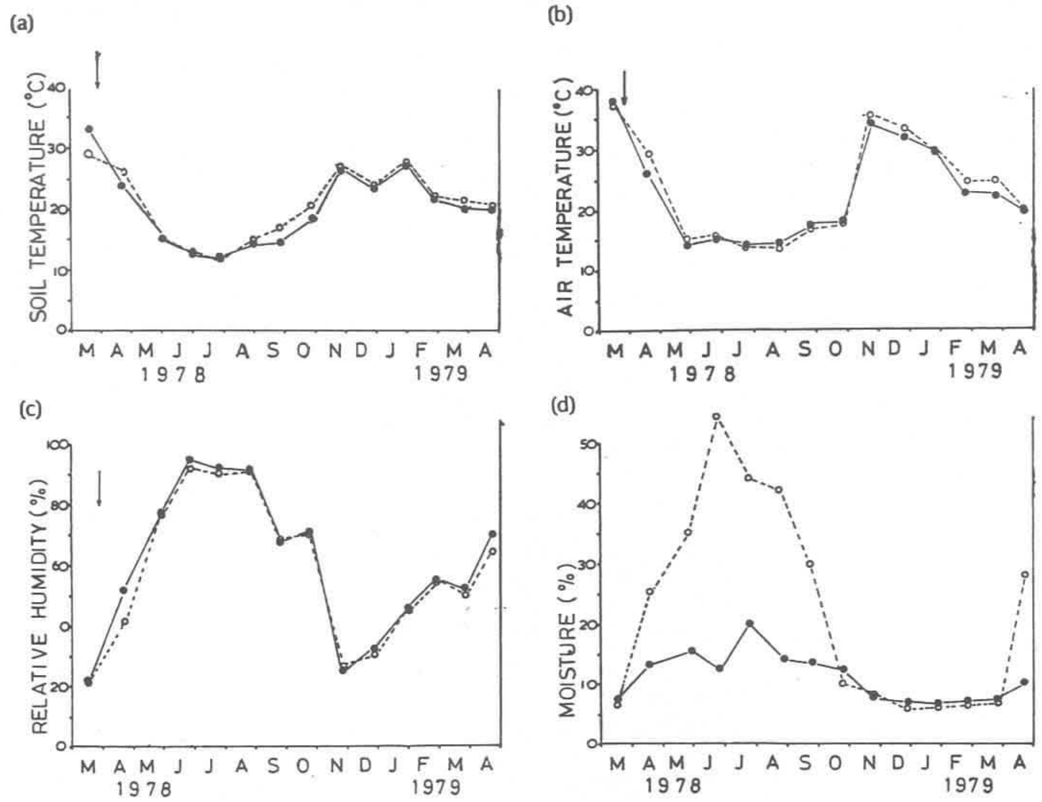

Fig. 3. Mean soil temperature at 5 cm depth (a), mean air temperature 5 cm above the soil surface (b) and mean relative humidity 5 cm above the ground (c) in the unburnt (●——●) and burnt (○--------○) plots at Karragullen. The arrow indicates date of burn. Graph (d) gives the percentage moisture of litter (○--------○ and soil (●——●) in the unburnt plot throughout the study period.

during April, August, September and October, 1978 and in March, 1979 ($p < 0.001$ using Students t-test). This trend was largely reflected by the air temperature (5 cm above ground) although burnt plot air temperature was lower than that of the unburnt plot between July to October, 1978 (Fig. 3b). Air temperature in the two plots significantly differed in April, August, November and December, 1978 and in February and March, 1979 ($p < 0.001$ using Students t-test).

Relative humidity was similar in the two plots prior to the fire but it decreased in the burnt plot relative to the unburnt plot following the fire (Fig. 3c). Inter-plot differences in relative humidity were significant in April, May, July and December, 1978 and in February and April, 1979 ($p < 0.001$ using Students t-test).

The unburnt plot trends in monthly soil and litter moisture (Fig. 3d) reflected that of rainfall (Fig. 2). Moisture variation within the litter was far greater than in the top-soil. Litter moisture level greatly exceeded that of the soil between April to September, 1979, although it was generally less than that of the soil between October, 1978 and March, 1979.

The pre-fire litter masses were comparable in the two plots (Fig. 4). The amount of litter was substantially reduced by the fire although it had commenced to build up by, or prior to, July, 1978 due to unnatural litter fall from the scorched overstorey crown. Litter continued to build up in the burnt plot and had attained 66% of the unburnt plot level by April, 1979.

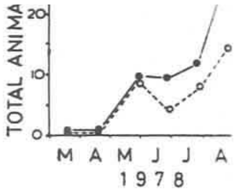

Fig. 5. Total soil and
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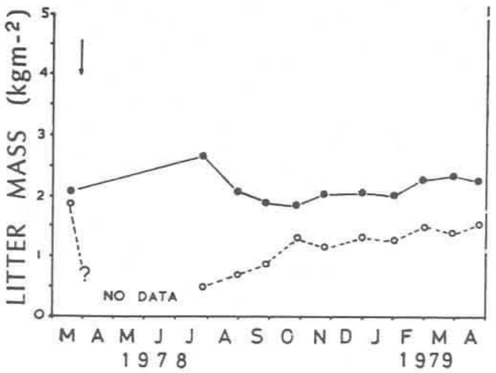

Fig. 4. Mean mass of litter (n = 10) in the unburnt (●———●) and burnt (○--------○) plots at Karragullen. Arrow indicates date of burn. Data were not collected in April, May and June, 1978.

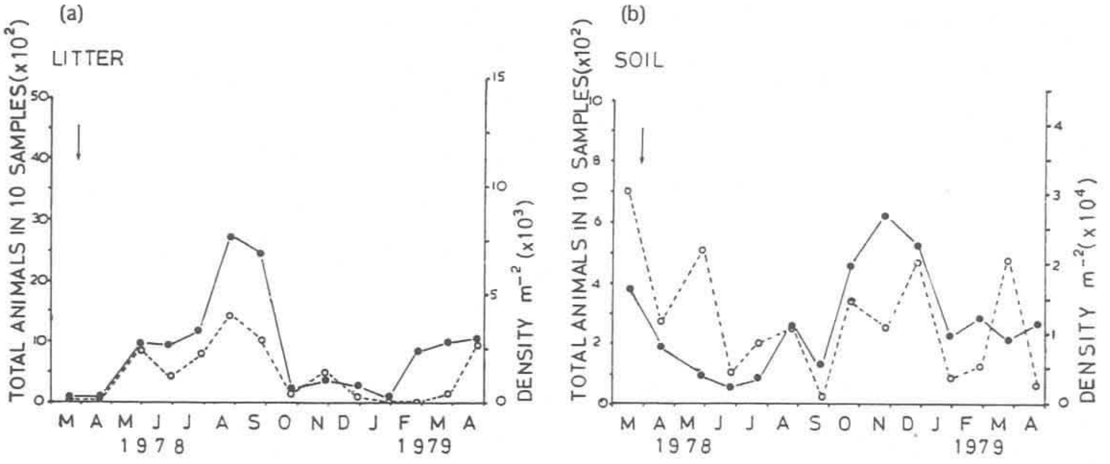

Fig. 5. Total soil and litter invertebrates sampled in the unburnt (●———●) and burnt (○--------○) plots at Karragullen. Arrow indicates date of burn.

3.2. Invertebrate samples

The total invertebrates sampled in the soil and litter during each month are shown in Figure 5. The information is presented as total animals in ten samples and also as population density m^{-2}. The individual taxa are presented separately in Figures 6—13. A number of additional taxa were sampled in the litter but were considered too sparse or infrequent to merit graphing. They are discussed below. Most taxa were strongly seasonal in their occurrence and, at least in the case of the soil samples, varied greatly in abundance between samples taken in a given month. In the following paragraphs a brief description of the trends exhibited by each taxon is given. Then, two methods are applied to assess the effects of the fire on the overall invertebrate community of the soil and the litter.

1. **Annelida** — Earthworms were only obtained from the litter and this was during the winter (Fig. 6a). The data were not adequate to elucidate trends clearly although it is worth noting that fewer worms were obtained from the burnt plot.
2. **Pseudoscorpionida** — There were no obvious effects on soil pseudoscorpions following the fire (Fig. 6b). With the exception of August, 1978, litter pseudoscorpion density was reduced following the fire and no appreciable recovery was observed by the end of the study period (Fig. 6c).

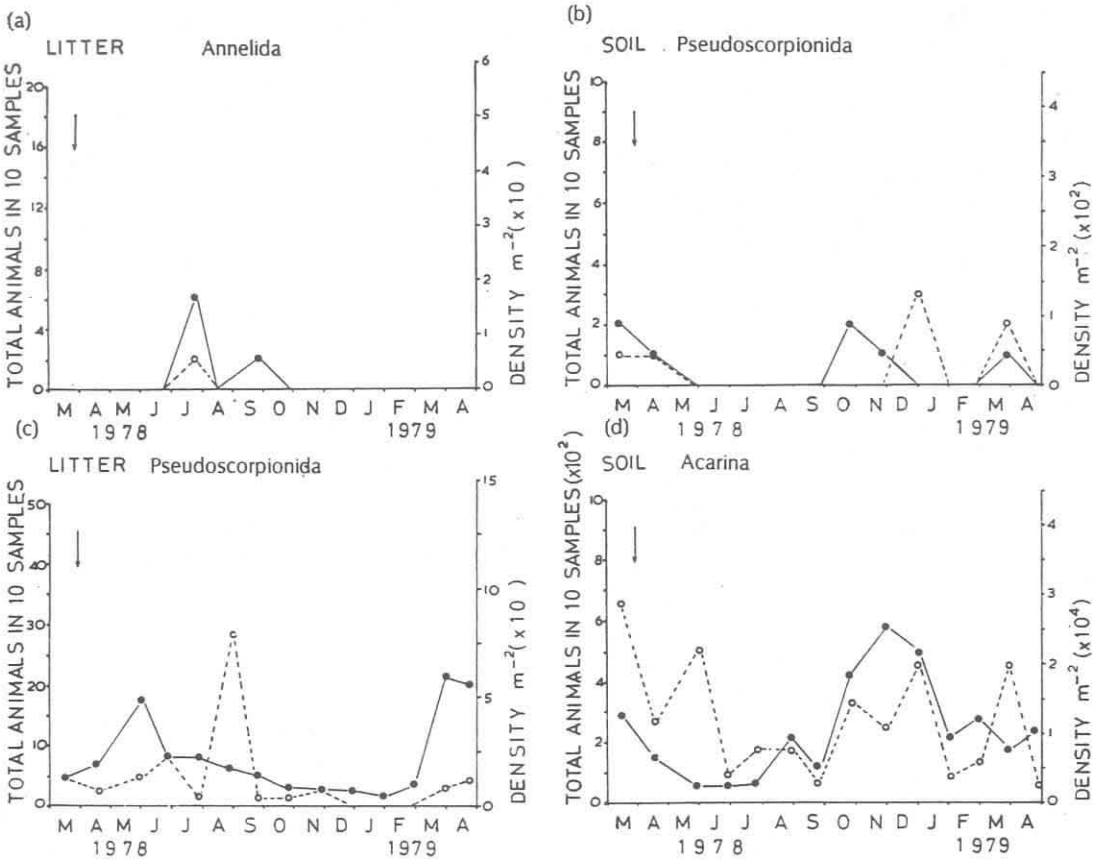

Fig. 6. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Annelida in litter, (b) Pseudoscorpionida in soil, (c) Pseudoscorpionida in litter and (d) Acarina in soil.

3. **Acarina** — Mites were the most abundant group in both soil and litter samples. The pre-fire mite density in the soil was greatest in the burnt plot (Fig. 6d). Density initially decreased following the fire although burnt plot densities did not decline to below unburnt plot levels until August, 1978. Thereafter burnt plot mite density remained the lowest for all but one of the remaining months of observation. Litter mite densities were initially comparable in the two plots (Fig. 7a). Burnt plot density values declined to less than those of the unburnt plot in December, 1979, when conditions were hot and dry. This difference persisted for the remainder of the observation period.

4. **Araneae** — Very few spiders were sampled in the soil, especially from that of the burnt plot (not graphed). Litter spider density was lowest in the burnt plot prior to the fire (Fig. 7b). Although this difference was maintained throughout the sampling period, it is uncertain how much the fire and how much base-line site differences influenced this result.

5. **Isopoda** — Few isopods were sampled in the soil (not graphed). A large winter peak of numbers was observed in the unburnt plot litter and the peak was substantially smaller in the burnt area (Fig. 7c).

6. **Diplopoda** — Millipedes were only abundant in the litter samples (Fig. 7d). Densities were moderately high in both plots although the peaks in June—July, 1978 and in February ro April, 1979 only occurred in the unburnt plot.

7. **Chilopoda** — Centipedes were seldom sampled in the soil (not graphed) but were found in the litter in all but the hottest months (Fig. 8a). There were no distinct differences in density between the two plots.

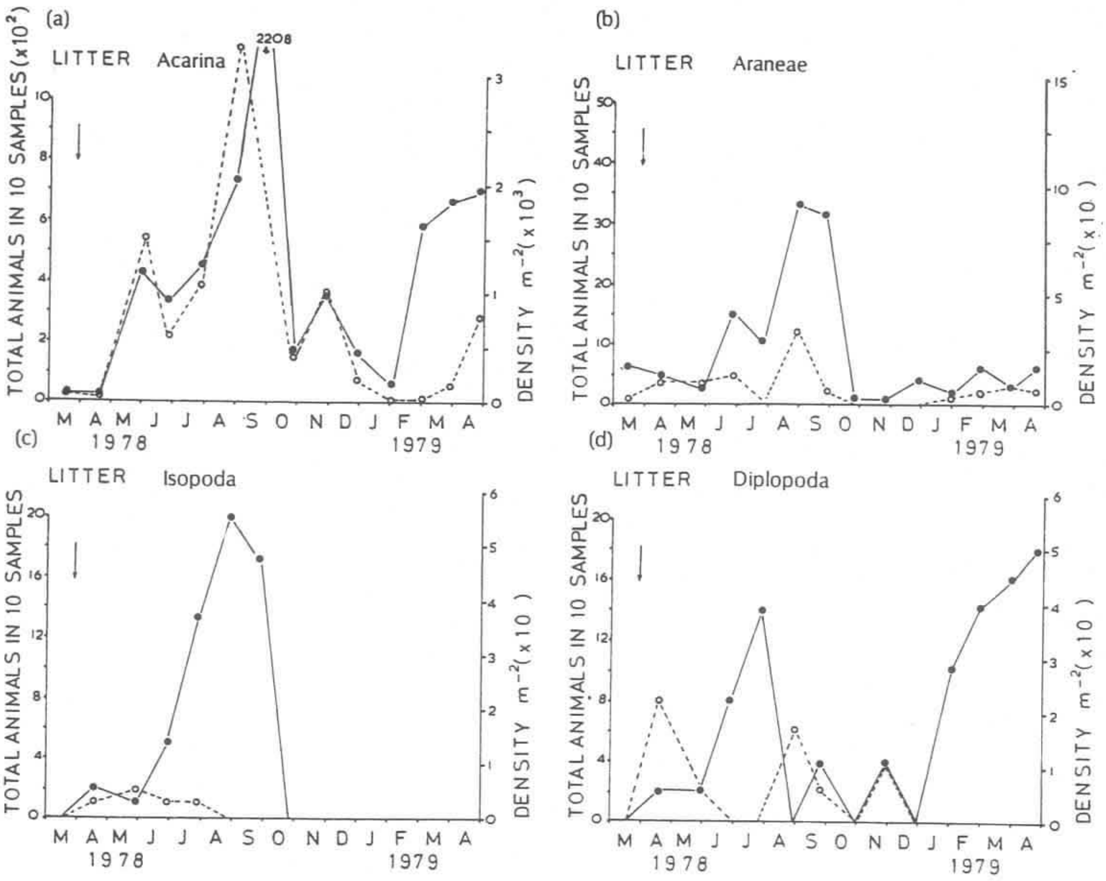

Fig. 7. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Acarina in litter, (b) Araneae in litter, (c) Isopoda in litter and (d) Diplopoda in litter.

8. **Symphyla** — These were regularly sampled in both the soil and litter but their density was only reduced after fire in the litter samples (Figs. 8b & 8c).

9. **Pauropoda** — Pauropods were only found once in the soil control plot soil samples (not graphed).

10. **Collembola** — Springtails constituted the second most abundant taxon of soil and litter. Prior to the fire the population density of the springtails in the burnt plot soil was lower than in the control plot (Fig. 8d). Fire apparently stimulated an increase in springtail density during winter when the burnt plot peak exceeded that of the unburnt area. Thereafter population density declined until a similar unburnt-burnt plot differential to that originally observed was obtained. By contrast the litter winter peak in springtails was lowest in the burnt plot although there was little difference in population density between the two plots from October, 1978 onwards (Fig. 9a).

11. **Diplura** — A few diplurans were sampled in the unburnt plot soil and the burnt plot litter between March—July, 1978 (not graphed). The data were not adequate to allow discussion of the effects of fire on this taxon.

12. **Thysanura** — A single specimen was sampled from the soil in the unburnt plot (not graphed) although these animals were abundant in the litter of both plots (Fig. 9b). Large seasonal fluctuations in catch hindered interpretation of the data although litter population density appeared to be depressed in the burnt plot from December, 1978 until the end of the sampling period.

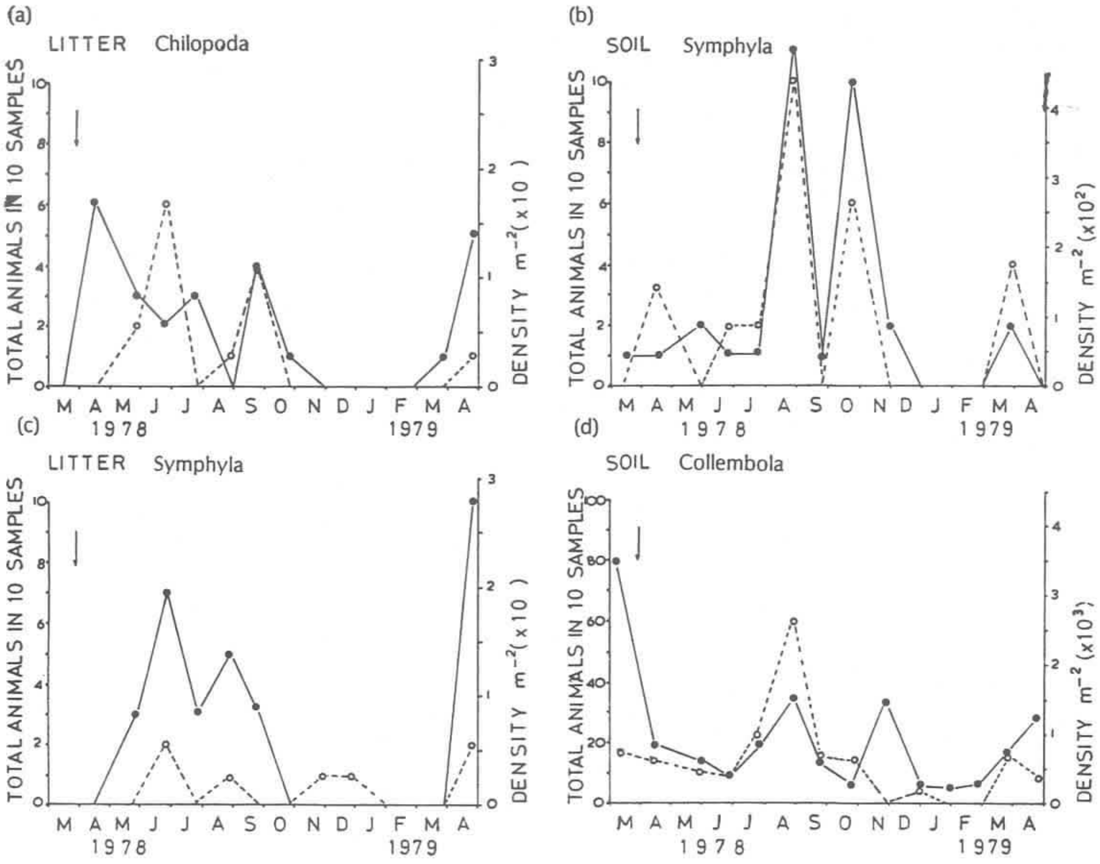

Fig. 8. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Chilopoda in litter, (b) Symphyla in soil, (c) Symphyla in litter and (d) Collembola in soil.

13. **Isoptera** — Termites fluctuated widely in the monthly samples of both litter and soil animals (Figs. 9c & 9d). This was probably caused by the patchy distribution of these social insects. No obvious effects of the fire on the soil catch were observed although termite occurrence in the litter layer appeared to be depressed in the early stages following the fire. Termites became more numerous in the April, 1979 litter samples from the burnt plot.

14. **Orthoptera** — Gryllidae and Acrididae were regularly sampled in the unburnt plot litter although none were sampled from the burnt plot (Fig. 10a). The absence of orthopterans in the pre-fire sample from the burnt plot appears to be an artefact since they were common here before the fire.

15. **Psocoptera** — These animals were sampled from both soil and litter during the warmer months (Fig. 10b & 10c). No clear effects of the fire were observed in either the soil or litter.

16. **Homoptera** — A few homopterans were sampled in the soil (not graphed) although they were relatively abundant in the litter layer (Fig. 10d). The fire had no obvious effect on their density in either the soil or litter layer.

17. **Heteroptera** — These were only sampled in the litter and density appeared to be substantially reduced following the fire for the duration of the observations (Fig. 11a).

18. **Thysanoptera** — Thrips were also only sampled from the litter and they were substantially reduced following the fire (Fig. 11b). A post-fire recovery appeared to have commenced around February, 1979.

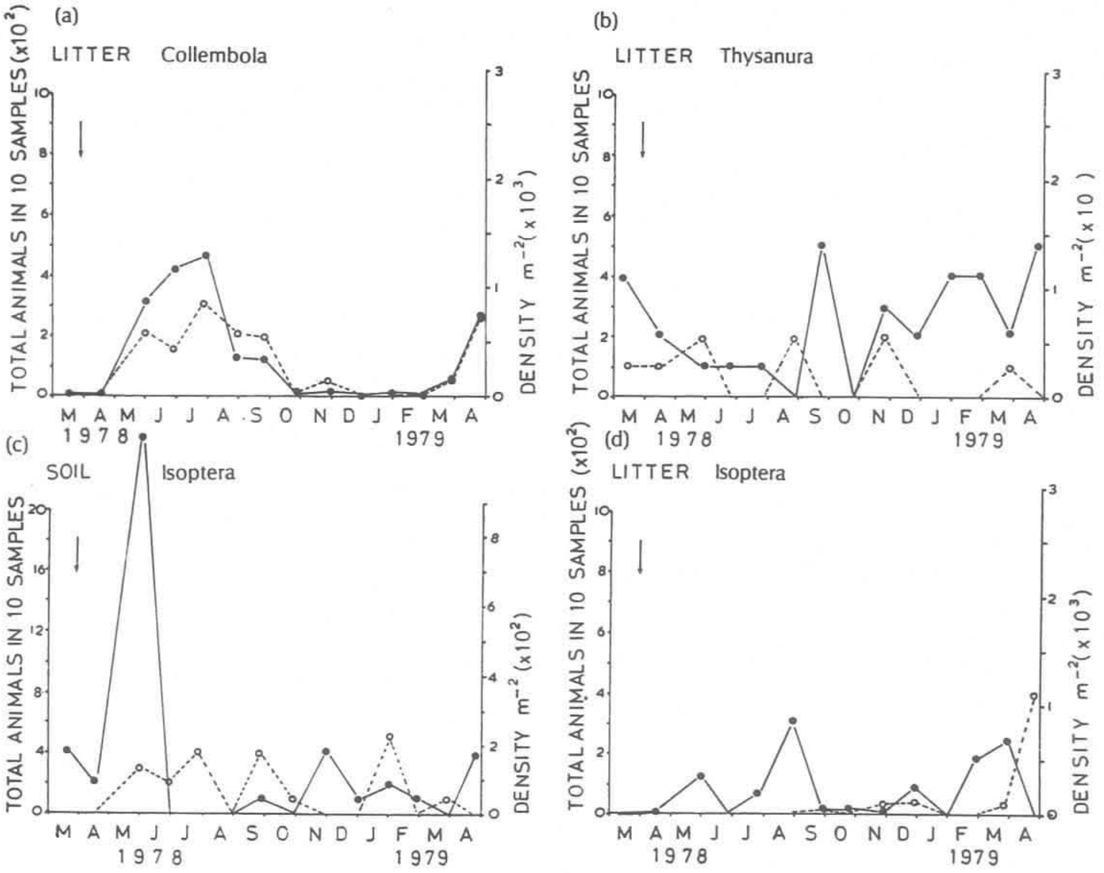

Fig. 9. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○-------○) at Karragullen. Arrow indicates date of burn. (a) Collembola in litter, (b) Thysanura in litter. (c) Isoptera in soil and (d) Isoptera in litter.

19. **Coleoptera** — The population density of adult and larval beetles appeared to be substantially reduced by the fire in both the soil and litter layer (Figs. 11c & 11d and 12a & 12b). Similar seasonal trends were observed in both plots and the post-fire litter density of adults appeared to be recovering from February, 1979 onwards. Larval density appeared to be building up in both substrates during early 1979.

20. **Diptera** — Adult and larval flies were sampled from the soil and litter of both plots (Figs. 12c & 12d and 13a). Adult Diptera were sampled in low numbers from the soil and are hence not graphed. No effects of fire on the soil Diptera were observed although both stages of the life cycle were reduced in the litter following the fire.

21. **Lepidoptera** — Very few Lepidoptera larvae were sampled in the soil (not graphed) although they were reasonably abundant in the litter (Fig. 13b). Here larval density appeared to have been reduced following the fire.

22. **Hymenoptera** — The data presented in Figure 13c are for wasps only; the information on ants will be presented in a separate paper (MAJER in preparation). Soil (not graphed) and litter (Fig. 13c) wasp population densities were low so the effects of fire may not reliably be described. It is noteworthy, however, that soil Hymenoptera were most consistently found in the burnt plot samples.

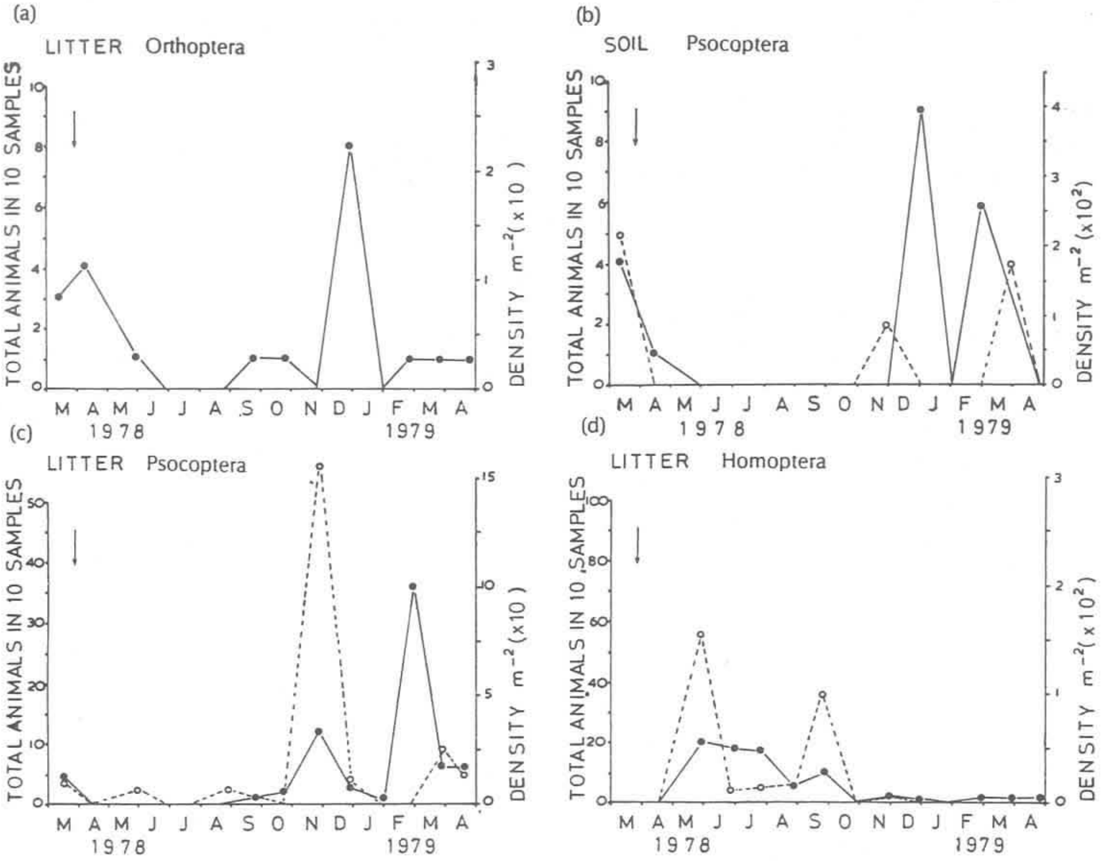

Fig. 10. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Orthoptera in litter, (b) Psocoptera in soil, (c) Psocoptera in litter and (d) Homoptera in litter.

In order to summarise the influence of fire on the fauna as a whole, each taxon was categorised in each month on whether numbers in the burnt plot were more (+), less (—) or equal (=) to those of the unburnt plot Tables 1a and 1b show the data presented in this way for the soil and litter samples respectively. The monthly counts of taxa in each of the above mentioned categories are also given. The number of taxa in the "+" and "—" category were then compared with the expected score using a "sign test" based on the Binomial distribution. On the null hypothesis that fire had no effect on the fauna each taxon was assumed to have an equal chance of being more or less abundant in the burnt plot. The "=" category was excluded from this analysis.

Prior to the fire the distribution of sign scores between taxa in the soil did not differ from that expected by chance (Table 1a) although for the same period in the burnt plot litter there were significantly more negative scores in the unburnt plot (Table 1b). Inspection of the litter taxa counts for the pre-burn sample (Figs. 6—13), however, indicated that numerical differences between the plots were low when compared with the post-fire situation.

There was no significant shift in the number of burnt plot soil fauna taxa showing a negative score until January, 1979, 9 months after the fire (Table 1a). This trend persisted, although not quite significantly due to the low number of taxa sampled, during February, 1979 but it was no longer apparent in the final two monthly samples.

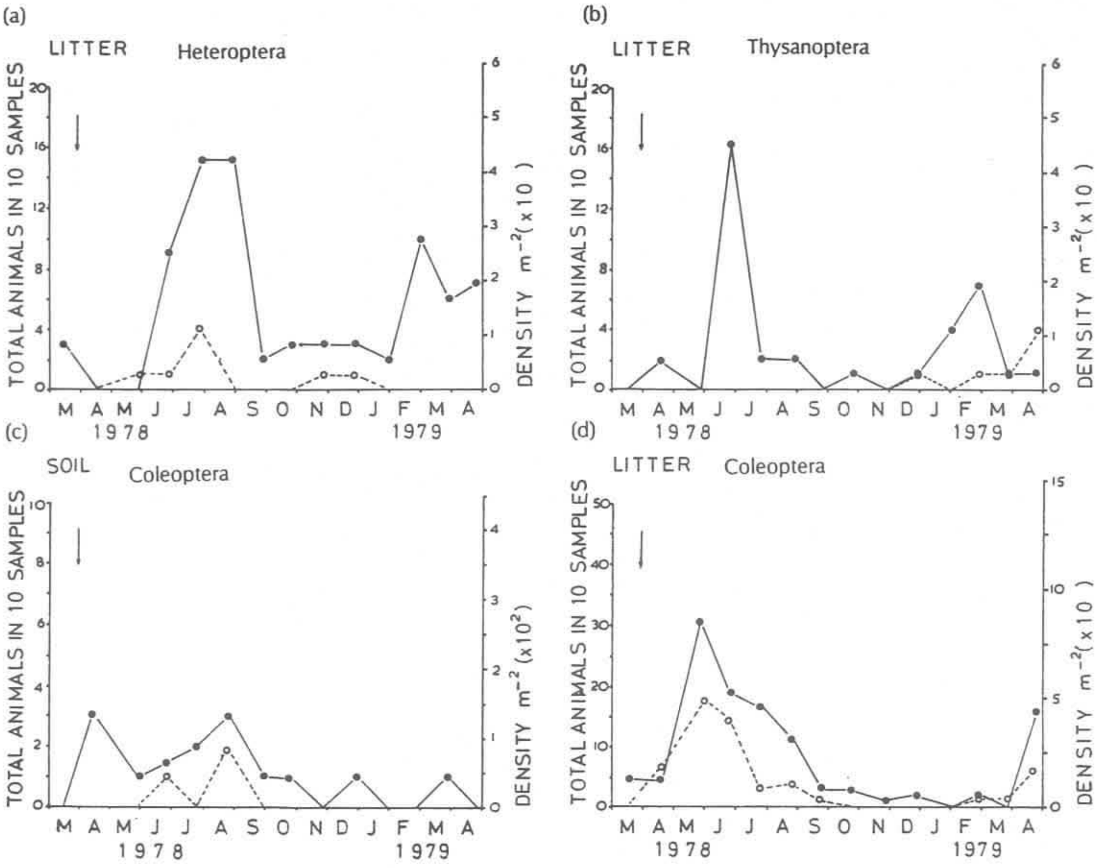

Fig. 11. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●——●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Heteroptera in litter, (b) Thysanoptera in litter, (c) Coleoptera in soil and (d) Coleoptera in litter.

Significantly more burnt plot litter fauna negative scores were observed during all but three post-fire samples (Table 1b). Since this was also the case prior to the fire, however, little meaning can be attached to this fact unless it is supported by other evidence.

Consideration of overall trends in faunal composition by the last method does not take into account the magnitude of the population density differences between plots. Principal components analysis (PCA) was therefore utilised as a method of simultaneously investigating the density changes of all taxa in the samples. The analysis was performed separately on the soil and litter fauna with the taxa scores standardised to unit variance in order to minimise the effect of the more abundant taxa. The taxa counts in the fourteen burnt and fourteen unburnt plot samples were compared using ORLOCI's (1966) weighted similarity coefficient (W.S.C.).

$$\text{W.S.C.} = \sum_{i=1}^{n} (xij - \bar{x}i)(xih - \bar{x}i)$$

(where xij, xih are the taxa scores for samples j & h, $\bar{x}i$ is the taxa score for the average sample and n is the number of samples). The technique then allows the samples to be arranged along axes, termed components, so that the samples with the least similar taxa content occur furthest apart. The first component, or axis, represents the combination of variables with maximum variance, subsequent components represent ones with lessening variance. The components may then be identified with environmental factors since these may contribute to the variation in taxa content. The use of PCA on sites which have been sequentially re-sampled through time is a relatively novel

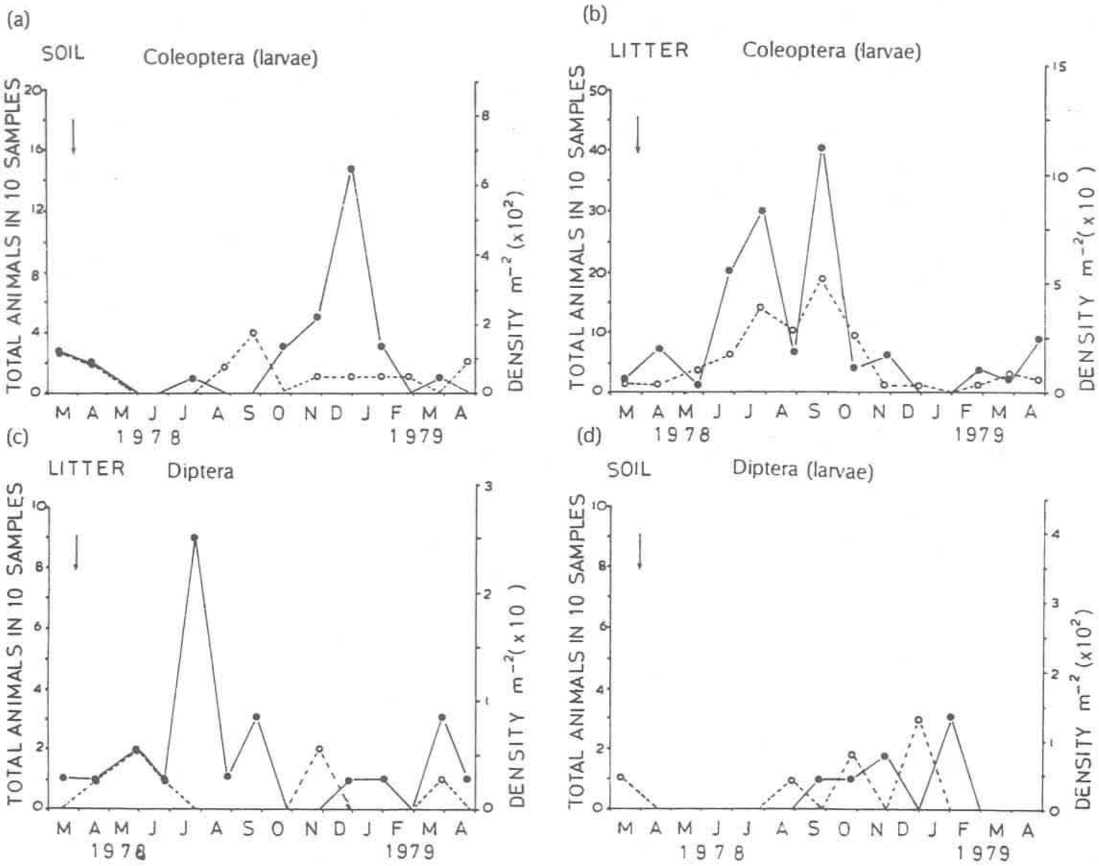

Fig. 12. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Coleoptera larvae in soil, (b) Coleoptera larvae in litter, (c) Diptera in litter and (d) Diptera larvae in soil.

application of this technique; other workers who have adopted this approach include Swaine & Greig-Smith (1980) who investigated change in grasslands following removal of sheep, and Posamentier *et al.* (1981) who investigated vegetation succession in heathland following a wildfire.

The post-fire successional trends of the soil and litter fauna are shown in Figures 14a & b respectively. In both cases the first axes, which respectively represented 16 and 25% variance of the soil and litter fauna, were most obviously associated with the effects of the fire. Seasonal effects also appeared to be represented on axis 1 of the litter fauna ordination (Fig. 14b). Changes in the sample scores are plotted against time. In the case of both soil and litter fauna the unburnt and burnt plot pre-fire samples had similar scores on axis 1 (Figs. 14a & b). This indicates, that, when abundance levels of each taxa were accounted for, the two plots were well paired with respect to soil and litter fauna density and composition. Immediately after the fire the position of burnt plot soil fauna samples diverged from the unburnt plot (Fig. 14a) although they generally followed the same seasonal trend. The burnt plot samples generally had a lower score on axis 1 than those of the unburnt plot although the situation reversed in August, 1978. The burnt and unburnt plot samples taken in February — April, 1979, about one year after the fire, received very similar scores on axis 1. This, together with the fact that the +/— scores of taxa were no longer significantly different in the March — April, 1979 samples (Table 1a) suggests that soil fauna had exhibited appreciable return to unburnt plot levels within 13 months after the fire.

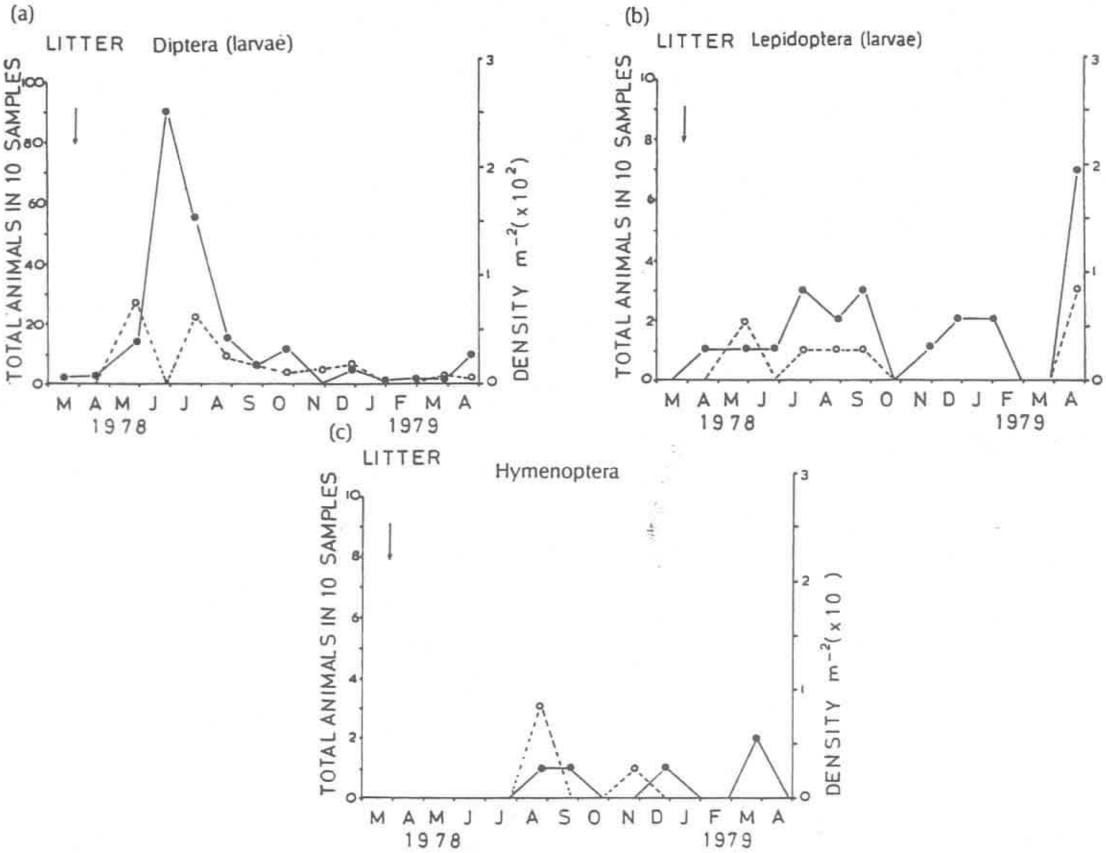

Fig. 13. Total soil and litter invertebrates from individual taxa sampled in the unburnt (●———●) and burnt plots (○--------○) at Karragullen. Arrow indicates date of burn. (a) Diptera larvae in litter, (b) Lepidoptera larvae in litter and (c) Hymenoptera in litter.

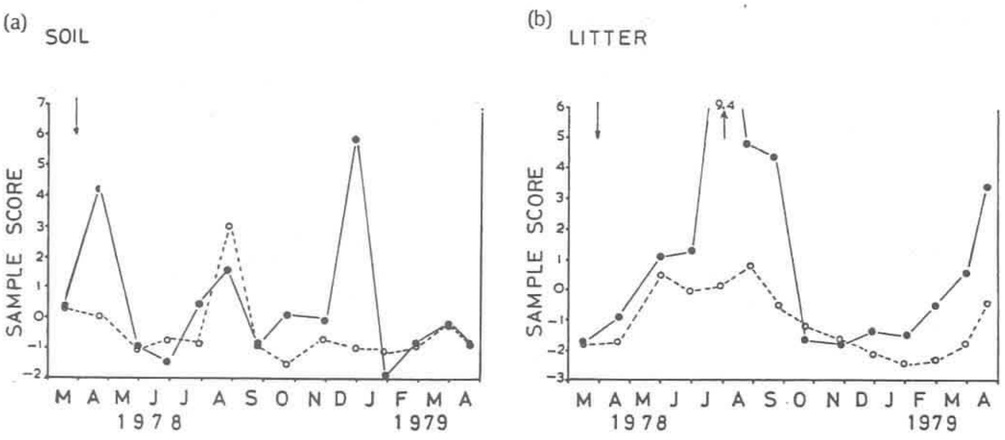

Fig. 14. Changes in sample score on the first axes of the soil fauna (a) and litter fauna (b) principal components analysis of monthly invertebrate collection data. Arrow indicates data of burn, (●———●) indicates unburnt plot, (○--------○ indicates burnt plot.

Table 1. Monthly breakdown of taxa sampled (1978—1979) in the (a) soil and (b) litter from unburnt and burnt plots showing whether each taxon was less abundant (—), more abundant (+) or equally abundant (=) in the burnt plot than in the unburnt plot. A nil entry means that the taxon was not found in that particular month. The signs are summarised in the table and differences from expected tested using a two-tailed "signs test" based on the Binomial distribution

			Sample date													
			Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Soil																
Arachnida	Pseudocorpionida		—	=						—	—	+			+	
Arachnida	Acarina		+	+	+	+	+	—	—	—	—	—	—	—	+	—
Arachnida	Araneae							—	—	—			—	—	=	
Crustacea	Isopoda			—				—								
Diplopoda				+						—						—
Chilopoda										+				—		
Pauropoda				—												
Symphyla			—	+	—	+	+	—	—	—	—				+	
Collembola			—	—	—	=	+	+	+	+	—	—	—	—	—	—
Diplura			—		—											
Insecta	Thysanura											—				
Insecta	Isoptera		—	—	—	+	+		+	+	—	—	+	—	+	—
Insecta	Psocoptera		+	—							+	—		—	+	
Insecta	Homoptera			=			—	+				—				
Insecta	Coleoptera			—	—	—	—	—	—	—		—			—	
Insecta	Coleoptera	(larvae)	=	=			—	+	+	—	—	—	—	+	—	+
Insecta	Diptera		+		+	—	—		+				—			
Insecta	Diptera	(larvae)	+					+	—	+	—	+	—			
Insecta	Lepidoptera	(larvae)								+			—			
Insecta	Hymenoptera				+	+	=	+	+		+	+				
Number of taxa which:																
are least abundant in burn plot			5	6	5	2	4	5	5	7	7	8	7	6	3	4
are most abundant in burn plot			4	3	3	4	4	5	5	5	2	3	1	1	5	1
exhibit no difference between plots			1	3	—	1	1	—	—	—	—	—	—	—	1	—
significance of deviation from expected			N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	***	N.S.	N.S.	N.S.

Litter

Annelida						—			—							
Onychophora						—										
Arachnida	Pseudoscorpionida		=	—	—	=	—	+	—	—	=	—	—	—	—	—
Arachnida	Opiliones						—									
Arachnida	Acarina		+	—	+	—	—	+	—	—	=	—	—	—	—	—
Arachnida	Araneae		—	—	+	—	—	—	—	—	—	—	—	—	=	—
Crustacea	Isopoda			—	+	—	—	—	—							
Diplopoda				+	=	—	—	+	—		=		—	—	—	—
Chilopoda				—	—	+	—	+	=	—					—	—
Symphyla					—	—	—	—			+	+				—
Collembola			—	=	—	—	—	+	+	+	+	—	—	—	—	+
Diplura							+									
Insecta	Thysanura		—	—	+	—	—	+	—		—	—	—	—	—	—
Insecta	Isoptera			—	—	—	—	—	=	—	+	—		—	—	+
Insecta	Orthoptera		—	—	—				—	—		—		—	—	—
Insecta	Psocoptera		—		+			+	=	—	+	+	—	—	+	—
Insecta	Homoptera				+	—	—	=	+		=	=		—	—	—
Insecta	Heteroptera		—		+	—	—	—	—	—	—	—	—	—	—	—
Insecta	Thysanoptera		—	+		—	—	—	—	—	—	=	—	—	=	—
Insecta	Coleoptera			+	—	—	—	—	—	—	—	—	—	—	+	=
Insecta	Coleoptera	(larvae)	—	—	+	—	—	+	—	+	—	+		—	+	—
Insecta	Diptera		—	=	=	=	—	—	—		+	—	—		—	—
Insecta	Diptera	(larvae)	—	—	+	—	—	—	=	—	+	+	=	=	+	—
Insecta	Lepidoptera	(larvae)		—	+	—	—	—	—		—	—	—			—
Insecta	Hymenoptera							+	—		+	—			—	
Number of taxa which:																
are least abundant in burn plot			10	12	7	17	19	10	15	11	7	12	12	14	12	16
are most abundant in burn plot			1	2	10	1	1	9	2	2	7	4	—	—	4	2
exhibit no difference between plots			1	2	2	2	—	1	4	—	4	2	1	1	2	1
significance of deviation from expected			**	**	N.S.	***	***	N.S.	***	**	N.S.	*	***	***	*	***

N.S. no significant difference; * $p < 0.1$; ** $p < 0.05$; *** $p < 0.005$

The burnt plot litter fauna scores diverged from those of the unburnt plot following the fire (Fig. 14b). Although both plots showed similar trends along axis 1 the later convergence, which was noted with the soil fauna, did not occur. By April, 1979 the two plots were still as separated on axis 1 as they had been 8 months earlier. This supports the suggestion raised by the results of the analysis of +/— taxa scores (Table 1b) that differences in population density and composition of the litter fauna in the two plots were still apparent 13 months after the fire.

4. Discussion

The current study is characterised by a number of strengths and limitations which merit further explanation. The low level of taxonomic separation inevitably obscures some effects of burning. This may be illustrated by the fact that DINDAL & METZ's (1977) investigation on Collembola in burnt areas revealed species which were either stimulated or reduced by fire. The danger of this broad taxonomic approach is further illustrated by BORNEMISSZA's (1969) survey of post-fire soil and litter fauna recovery in Western Australian woodlands; his data suggested that numerical recovery took less than three years. SPRINGETT's (1971) work in nearby pine plantations showed that although recovery appeared to be complete within three years if a broad taxonomic approach was considered, the effects of fires were apparent after this time if a more sensitive identification of fauna at the taxonomic or trophic level was utilized.

An additional problem is that both of the present study plots had been burnt 2.5 years before commencement of this study. SPRINGETT (1976) concluded that the diversity and population density of soil and litter fauna was still affected by fire at the end of a 5—7 year prescription burning rotation. This means that the fauna of both plots was probably already affected by the previous fire. One additional limitation of this study is that it only looked at the short-term effects of fire. Various workers (e.g. LUSSENHOP 1976, MAIN 1981) have noted immediate and longer-term effects of fire and the present study may not cover some of the later category of changes.

The study contributes three advances over previous Western Australian fire — soil and litter invertebrate studies. First it includes pre-fire samples — a desirable feature already called for by CAMBELL & TANTON (1981). In addition, it separately considers the effects of fire on the soil and litter fauna. Finally, the study enables the time sequence of responses to fire to be investigated over a 13 month period.

The fire caused a series of environmental changes which had not completely recovered by 13 months after the fire. For instance, plant ground cover density was reduced from a mean of 57% to 0% by the fire and had only grown back to 36% by the end of the observations (MAJER unpublished data). The build up of litter mass followed a similar trend (Fig. 4) and quantitative recovery was not complete after 13 months. The burnt plot litter also differed from unburnt litter in terms of its chemical and physical composition. Associated with these changes in vegetation and litter were microclimatic effects. The fire resulted in an increased soil and air (5 cm above ground) temperature and a reduced relative humidity (Figs. 3a, b & c).

These effects were probably caused by the lack of insulating vegetation and litter and by the increased solar absorbance of the blackened ground. Although only measured in the unburnt plot, it is also probable that soil and litter moisture levels were reduced by the effects of the fire.

The fauna may be influenced by the direct physical effects of the fire or by longer-term changes in factors such as food availability, shelter and environmental conditions (MAIN 1981). Surprisingly few taxa exhibited obvious effects of fire in the immediate post-fire sample. The few examples include soil Acarina and litter Pseudoscorpionida, Isoptera and Coleoptera (larvae). This partly results from the fact that many taxa were not present in the litter or upper soil horizons in the adult or larval stage at the time of the fire.

Longer-term effects were more common although, as observed by DINDAL & METZ (1977), the taxa exhibited a variety of response types. Taxa on which fire had a nil or very slight effect included soil Pseudoscorpionida, Chilopoda, Symphyla, Isoptera, Psocoptera, Homoptera and Diptera (adults and larvae) and also litter Psocoptera and Homoptera. A second category exhibited a seasonal build up after the burn which was of lower magnitude in the burnt than the unburnt plot. Included here were the soil Isopoda and Coleoptera and the litter Araneae, Diplopoda, Symphyla, Collembola, Thysanura, Orthoptera, Heteroptera, Thysanoptera, Coleoptera (adults and larvae), Diptera (adults and larvae) and Lepidoptera. An extreme case of this category was those taxa which failed to occur in the burnt plot but which exhibited post-fire peaks in the unburnt plot. Included here were the soil Araneae and the litter Annelida and Isopoda. Three taxa which did not fit into these categories were the litter Acarina, which were reduced by the fire after a long time lag, the soil Collembola, which were initially stimulated but later declined following the fire, and the soil Hymenoptera, which may have been stimulated by the fire. It should be stressed that all responses are for the aggregate of species contained within the class or order; each broad taxon may contain species exhibiting a variety of responses.

It is noteworthy that the majority of taxa on which fire had little or no effect were those sampled in the soil whereas the taxa which were substantially affected by fire were those from the litter. This suggests that fire had a greater impact on litter fauna than on that of the soil. Furthermore, the PCA (Fig. 14) suggested that soil fauna had undergone considerably more recovery than the litter fauna by 13 months after the fire. These findings are in keeping with those of SPRINGETT (1979) who investigated the effects of fire on two Jarrah forest millipedes, *Podykipus* sp., a surface-living species, and *Atelomastix* sp., a burrowing species. Samples taken 14 – 16 months after the fire indicated similar, or sometimes greater numbers, of *Atelomastix* sp. in the burnt plots to that in the unburnt areas. By contrast numbers of the surface-living species were lower in all burnt plots than in the unburnt areas. The present results and those described by SPRINGETT (1979) probably result from the fact that fire causes more physical and chemical alteration of the litter layer than that of the upper soil horizons.

Although litter in the burnt plot had built up to 66% of the mass in unburnt areas by the end of the observation period, its composition was extremely different. The burnt plot litter was largely devoid of fine litter fragments, as noted for other recently burnt areas (HATCH 1955). The 02 layer of decomposing litter (see SPECHT 1981) was poorly formed and was not yet colonised by many of the microorganisms which form the food source of certain invertebrates (MACAULEY 1979, D. FRASER personal communication). Thus, in the burnt plot, the litter was qualitatively and quantitatively less suitable for many components of the litter fauna.

There has been some dispute over the impact of fire on soil and litter fauna. SPRINGETT (1976), using the plot comparison approach with no pre-fire data, concluded that fire reduced the soil species richness and fauna density and that recovery was incomplete by the time of the next 5—7 year rotational prescription burn. CAMPBELL & TANTON's (1981) detailed analysis of pre- and post-fire litter data from a selection of plots in the Australian Capital Territory indicated that spatial and temporal variations in data were so great that the effects of fire could not be confidently assessed from a post-fire comparison of one unburnt and one burnt plot using low sample sizes. CAMPBELL & TANTON (1981) extended their discussion to cast doubt on SPRINGETT's (1976) findings. The present study makes no comment on species richness (neither did CAMPBELL & TANTON) but it does contribute to the debate on faunal density. It conclusively demonstrates that the density of many litter-living and some soil-living taxa was reduced at some time or other during the 13 month post-fire observation period. There are distinct differences in rates of recovery of soil and litter fauna and indeed of individual taxa. The range of responses to fire also complicates the issue. However it may be concluded that fire affects the density of many soil and litter dwelling taxa and that the effects of fire are still apparent in the litter fauna, and to a lesser extent the soil fauna, 13 months after the fire.

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Synopsis: *Original scientific paper*

MAJER, J. D., 1984. Short-term responses of soil and litter invertebrates to a cool autumn burn in Jarrah *(Eucalyptus marginata)* forest in Western Australia. Pedobiologia **26**, 229—247

Soil and litter fauna densities, litter biomass, and certain microclimatic parameters were monitored monthly for 1 month prior to, and 13 months after, a cool autumn burn in eucalyptus forest. Samples were taken simultaneously from a similar, but unburnt, plot.

Litter biomass dropped considerably following the fire and had built up to 66 % of the unburnt plot level after 13 months. Burning resulted in a generally increased soil and air temperature and a reduced relative humidity at ground level.

The soil and litter invertebrates, when considered at the broad taxonomic level, exhibited a range of responses to fire. These included immediate density reduction, delayed density reduction, temporary absence following fire, density stimulation or unaffected by fire.

The behaviour of the soil fauna and litter fauna were both assessed using simple binomial signs tests and by principal components analysis. The analyses demonstrated that fire affects the density of both soil and litter fauna and that the effects of fire were still apparent in the litter fauna, and to a lesser extent the soil fauna, 13 months after the fire.

Key words: prescription burn, fire, soil fauna, litter fauna, litter mass, microclimate, forest litter, Eucalyptus marginata.